

Ornithology from the lakeshore

THE EVOLUTION OF ADVERTISING

This issue of *Ardea* contains a review of a book entitled 'The evolution of beauty: how Darwin's forgotten theory of mate choice shapes the animal world – and us'. The book is written by Richard O. Prum, professor in ornithology at Yale University. Because it is about sexual selection, my prime research interest, I felt I needed to read it. And after reading it, I felt I needed to (ab)use this editorial to discuss it. An editorial is not the same as a book review, but you'll have to forgive my diatribe.

Readers of *Ardea* will need no convincing that birds are the most wonderfully diverse and beautiful creatures on the planet. A fundamental biological question is why this is so; more precisely, how did these 'ornamental traits' – this beauty, if you wish – evolve? As any textbook in animal behaviour or behavioural ecology will tell you, it was Darwin who came up with an explanation. Darwin realized that his theory of natural selection only explained the evolution of traits that increase an organism's chance of survival, and that ornamental traits such as beautiful song and gaudy plumage might rather do the opposite. So, Darwin proposed the theory of sexual selection, which explains the evolution of traits that increase an individual's chances of obtaining one or more mates to reproduce. The agents of sexual selection are the sexual rivals and potential mates. Being unsuccessful or less successful does not mean organismal death, but evolutionary death (no or fewer offspring). Darwin recognized that there are two processes at work: intra-sexual selection (competition) leading to selection of traits such as weaponry and large body size, and inter-sexual selection (mate choice) which selects for traits that enhance attraction by members of the opposite sex.

We can be grateful for inter-sexual selection, because it led to avian beauty. But as Malte Andersson wrote in his book 'Sexual selection' in 1994 "the evolution of female preferences remains controversial", and that is still true today. Without going into details, several hypotheses have been proposed, including direct benefits to choosy individuals, sensory bias (selection on the sensory system in another context than mate choice), selection for species recognition (and hence avoiding hybridization), genetic indicator mechanisms and Fisherian self-reinforcing selection. Andersson noted that these explanations "are all compatible and may apply in combinations". Now comes Prum's book. He argues that virtually all evolutionary biologists have betrayed Darwin and have followed Wallace in

believing that mate choice is adaptive. Prum seems truly upset by Zahavi's 'handicap principle', which suggests – with other indicator models – that individuals can judge the underlying quality of a potential mate through the expression of the (costly) ornament. Prum calls it "antiaesthetic sexual biology" (R.I.P. Amotz).

Reading the book, it felt like Prum rants and raves against anyone who even entertains the idea that the handicap hypothesis or indirect 'good genes' benefits of mate choice might be valid, including Alan Grafen, Richard Dawkins, and most of the rest of us lesser mortals. The poor evolutionary psychologists are hit the hardest – and even below the belt –, but *Ardea* is an ornithological journal, so I gladly refrain from further discussing what Prum has to say about humans.

I like reading books and I greatly admire people – including Prum – who write well. I much enjoyed the personal accounts of birding trips and travels, the detailed descriptions of natural history including the courtship displays of manakins and bowerbirds he and others observed, and the celebratory narratives of his own research or that of his students and collaborators on duck penises, manakin wing bones and dinosaur plumage colour. His personal stories of success and failure (mostly success of course) are coloured, but also colourful and worth reading. The natural history descriptions made me reminisce about my own experience of the thrill of watching behaviours not yet described or understood.

When it comes to Prum's 'Beauty Happens' hypothesis on aesthetic evolution, I am genuinely interested in understanding his ideas, but am baffled by his arguments. Prum contends that there is a lot of bad science out there and that "adaptive mate choice explanations often seem like Rudyard Kipling's 'Just So Stories'", and he laments about unreproducible results and null results hidden in file drawers. He writes "Many studies have failed to find any evidence of a correlation between good genes and female sexual preferences". Fair enough. But all these *valid* concerns seem to be raised only when it comes to tests of alternative hypotheses that do not fit with Prum's pet idea. In his discussion of evidence in favour of Beauty Happens, issues about scientific quality and rigour have gone out of the window. What follows are unbalanced and uncritical statements, and a book filled with just so stories. The expression 'the pot calling the kettle black' sums it up well.

Or what to think of this example about why female ducks so strongly refuse forced copulations. “What is at stake... is more than just the *direct cost* to the female’s health and well-being; forced fertilizations will also create *indirect, genetic costs*... that may be even more important to the female”. Females that do not have their offspring sired by their preferred mate “will have offspring that are sired by males that have random display traits, or traits that have been specifically rejected because they have failed to meet female aesthetic standards” and this “will result in fewer grandchildren for that female”. May I politely ask for evidence? Prum asks us to consider the sexy-son hypothesis (which I’m happy to do), but why should we then not consider the ‘good genes’ hypothesis? Based on which evidence should we accept the existence of sexy-son benefits but deny females any ‘good genes’ benefits? Why should we stop investigating whether males that can defend a central position on the lek day-in-day-out are healthier or less inbred than those that surround them?

The book also contains too many flawed or failed comparisons. Some simply didn’t work for me, such as comparing the Fisherian process with conflict resolution in a marriage. Others are instructively questionable. To compare the null model of Beauty Happens with the adaptive mate choice model (honest indicators), Prum writes “After all, a Maserati or a Rolex can be aesthetically pleasing while also performing utilitarian functions like driving... or keeping accurate time”. Isn’t this somewhat beside the point? Doesn’t the owner of a Maserati or a Rolex signal (quite honestly) that he or she is wealthy and aren’t these aesthetically pleasing objects then honest indicators of the possession of financial resources that might be useful in the context of reproduction? There are a few key questions here. Would we find these ‘beautiful’ Ferraris, Lamborghinis, Rolls Royces, and now Teslas as aesthetically pleasing and interesting if they would cost a fraction of what they do now, that is, if everyone and their uncle could afford these luxury cars? Do the owners of such cars only attract a partner because they have this beautiful car and the choosing individual is ‘aesthetically pleased’? Finally, some comparisons are easily made, but not necessarily valid, such as the one about the stock market: “Both sexual displays and asset prices can be driven by popularity alone, decoupled from extrinsic sources of value”.

Prum’s book is depressingly unscientific. It is an advertising pamphlet – “Only the Beauty Happens hypothesis allows for a genuine engagement with the full, explosive diversity of sexual ornament” – with

some remarkable arguments why we need to accept its main hypothesis. Argument one is that Beauty Happens (in more technical terms the Lande-Kirkpatrick model) is “the appropriate null model for the evolution of traits and preferences” and thus “it cannot be proven”. Demanding proof is thus demanding *the impossible* (emphasis by Prum). Ironically, a few paragraphs earlier Prum writes that adaptive mate choice “is mostly just a belief that the world *must* be that way”. According to Prum, “The only way for evolutionary biologists to proceed is to embrace the Beauty Happens mechanism as the null model”. To be fair, I believe that Prum is right when he argues that the null hypothesis (“there is actually nothing special going on”) deserves better treatment (see Ioannidis 2005). I recommend Forstmeier *et al.* (2016) for a practical guide. As to mate choice, I suggest we take one more step back and ask how strong the evidence is that females prefer a particular male based on the expression of his (beautiful) ornaments. Argument two is essentially that we do not need data. Prum admits that “studying mate choice in the Great Argus (a polygynous pheasant of stunning beauty) in the wild would be extremely difficult”. After some just so stories, he then writes, “In conclusion, even without further data from the wild, there are excellent reasons to think that the Great Argus is an evolutionary example of the Beauty Happens mechanism”. Q.E.D. Argument three is equally baffling. Prum reasons that the lack of papers supporting his idea is... proof of the idea. He writes, “The scantiness of the published research likely points to reams of unpublished evidence that would support the Beauty Happens mechanism if they were ever to see the light of day”. A very different, but equally telling statement about how Prum approaches scientific evidence is about models. He informs us that, “Sam Snow and I are developing a mathematical, genetic model that will establish the efficacy of the aesthetic remodeling mechanism as proposed in bowerbirds, manakins and humans”. Whenever you come up with a hypothesis, you simply have to work hard until you have developed the model that will confirm it. If so, I would definitely understand Zahavi’s disdain for mathematical models. The final argument is simply bewildering: evolutionary biology should “adopt the nonadaptive, Beauty Happens null model” and “restore the Darwinian view...” “...to sever our historical connections to eugenics”. “Adopting the Beauty Happens null model breaks *the logical inevitability of eugenic thought*” (my emphasis). These ‘arguments’ as well as Prum’s way of ignoring or giving short shrift to any study that doesn’t fit his worldview, seem to have an early origin:

describing his first year in graduate school (“This was my first exposure to the science of mate choice”) he writes, “But even then I could sense that the open-ended and arbitrary qualities of the Fisher hypothesis looked a lot more like how nature worked than the honest signaling theories did”.

Prum claims that, “most of those who think of themselves as Darwinians today have gotten Darwin all wrong”, and then adds that, “the Darwinian theory of mate choice has largely been suppressed, misinterpreted, redefined, and forgotten in science”. Really? Wait, it gets better. Prum writes, “Wallace set in motion the transformation of Darwin’s fertile, creative, and diverse intellectual legacy into the monolithic and intellectually impoverished theory with which he is almost universally associated today”. Then, Prum goes on to explain how we have to understand Darwin. “If Beauty Happens, then sexual display traits do not always improve survival, and can instead evolve to be highly costly to the individuals that have them”, and “survival is not the only priority in life when sexual success is determined by mate choice”. Yes, indeed, isn’t that the whole point of why we need a theory of sexual selection and isn’t this textbook knowledge? Prum also talks at length about the “transformative power of female mate choice”. Yes, indeed, any textbook will tell you that that’s one of the two key processes of sexual selection. He also writes in one of the later chapters, “If you were educated to think that evolution is synonymous with adaptation by natural selection and the persistent improvement of the species, then the evolution of aesthetic decadence may seem troubling”. So, who is his audience that has been educated to think like that? I cannot help feeling that this book is the outcome of Prum’s personal war against a battalion of self-created straw men (and women).

Prum seems happy that his finding in waterfowl “is a profoundly feminist scientific discovery”. (By the way, this finding is not as new as it may seem from his account: similar conclusions about sexual conflict have been drawn from work done decades ago on the male and female reproductive organs of dragonflies and on *Drosophila* mating). When reading this and other essays from evolutionary biologists with an obvious political agenda or profound personal experiences that are closely related to the research topic, I am convinced behavioural ecology does far better when it is kept free from politics and moral values. Is it inevitable or desirable that answers to questions about whether female birds obtain indirect ‘good genes’ benefit from their choice or not, whether mate choice is adaptive or not, or whether males or females are in control of mating

have any bearing on our laws, our moral views and values, our opinions about human rights? I sincerely hope not.

There is a lot more to say about the ideas and statements presented in this book, but I’ll leave it to one final example. Prum writes that “the experience of mate choice is... pleasurable, something that is still rarely acknowledged in the scientific literature on mate choice” (he also adds “Darwin, however, proposed it”). And if you don’t acknowledge this, then according to Prum “the result is sanitized sexual science”. First, I want to know how we know that mate choice is pleasurable and second, can anyone please explain why this would be important in the context of sexual selection and the evolution of beauty? I like to believe that pleasure, lust, love, jealousy, anger and so on all exist in birds too (and generally in other animals than humans) – and there might be indirect ways to find out, now or later – but then what? If a male sees a rival in his territory near his fertile female, does it matter whether he is angry or jealous or whether it is another neurobiological mechanism that will lead him to kick the rival out of his territory? If a male and female albatross form a life-long pair after a long courtship period, does it matter whether what they experience is love or pleasure or something else? Given how rarely they do it, perhaps a female manakin feels relief after she has finally finished the copulation business, but what does that tell us?

In the end, I was left with the feeling that whoever fails to embrace the true teachings of Darwin as enlightened to us by Prum is a failed evolutionary biologist (or even human being) and obviously on the wrong path. Apart from the wonderful descriptions of natural history and behaviour, Prum’s personal accounts of birding and scientific discovery, and the bird photos inside, I find the ‘Evolution of beauty’ not a beautiful book. Although I agree with Prum that, “The adaptationist worldview can make us blind to the true nature of reality”, this true nature of reality here seems equivalent to Prum’s reality. He is entitled to it, but as a scientist I remain hopeful that advertising and fake news will lose eventually and that the scientific enterprise will continue to move us closer to the true, evidence-based reality. To me, that’s where the real beauty lies.

Forstmeier W., Wagenmakers E.-J. & Parker T.H. 2016. Detecting and avoiding likely false-positive findings – a practical guide. *Biol. Rev.* 92: 1941–1968.

Ioannidis J.P.A. 2005. Why most published research findings are false. *PLoS Med.* 2: 696–701.

Bart Kempenaers